

Studies on pollen fertility restoration in three CMS lines carrying *Cajanus cajanifolius* cytoplasm under four diverse environments

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ABSTRACT

Stability of pollen fertility was studied in 102 pigeonpea [*Cajanus cajan* (L.) Millsp.] cross combinations in four environments. The data, as revealed by aceto-carmin test, showed that pollen fertility of the hybrids varied considerably across the locations and three CMS lines used in crosses. None of the testers maintained complete male sterility, but partial male sterility restoration was frequent. The stability analysis revealed that nine hybrids derived by crossing ICPA 2043, four by ICPA 2047, and three by ICPA 2092 were highly stable for fertility restoration across the four environments. Seven genotypes viz., AKT 8811, BSMR 736, TV 1, BSMR 846, PHULE T-4-1-3-1, ICPL 20106 and ICP 3514 were identified as potential male parents for breeding pigeonpea hybrids with stable fertility restoration.

Key words: CMS lines, Maintainer, Pigeonpea hybrid, Restorer, Stability, Testers

Male sterility is considered a unique biological gift of nature. This single genetic phenomenon has played a very significant role in combating global hunger through its direct use in the exploitation of hybrid vigour; and thereby, enhancing the crop productivity by significant tonnage. Since the discovery of male sterile plants with impaired anthers by Kolreuter (1763) tremendous efforts have been made to understand, characterize and utilize the male sterility system for yield enhancement in various crops. The highly benefitted crops using the male sterility systems are maize (*Zea mays*), sorghum (*Sorghum bicolor*), pearl millet (*Pennisetum glaucum*), rice (*Oryza sativa*), cotton (*Gossypium hirsutum* spp.), castor (*Ricinus communis*), sunflower (*Helianthus annuus*) and a number of horticultural crops. Unfortunately, no legume crop appears in this elite group; and it is due to their reproductive limitations in producing cost effective cross-pollinated (hybrid) seeds. However, an exception to this is pigeonpea [*Cajanus cajan* (L.) Millsp.]. In this crop the insect-aided natural cross-pollination is sufficiently high to produce bulk quantities of hybrid seed (Howard *et al.* 1919). Breeding hybrid cultivars in this crop could not be launched due to lack of any male sterility system. A breakthrough in this direction was achieved when Saxena *et al.* (2005) reported the development of a stable cytoplasmic nuclear male sterility system; and this cleared the deck for breeding hybrids in pigeonpea. The breeders so far have released

three commercial pigeonpea hybrids with over 30% yield advantage in farmers' fields (Saxena and Tikle 2015). To sustain the hybrid pigeonpea breeding technology, it is imperative that new high yielding hybrids are made available to the farmers at a regular pace. This can only be achieved if new male parental lines with ability to restore pollen fertility of hybrid plants under diverse environments are developed. In the present study, therefore, efforts were made to select promising fertility restorer lines using three different CMS lines and four environments.

MATERIALS AND METHODS

The experimental materials used in this study involved three CMS lines (ICPA 2043, ICPA 2047 and ICPA 2092) carrying A_4 (*Cajanus cajanifolius*) cytoplasm (Saxena *et al.* 2005) and 34 testers (male parents). The group of testers comprised of 13 genotypes from ICRISAT; 10 genotypes from Agricultural Research Station, Badnapur; five from Agricultural University, Rahuri and six from Agricultural University, Akola. One hundred and two crosses were made in a line x tester mating design at the Agricultural University at Parbhani. All the F_1 s were sown in a randomized complete block design in two replications at Patancheru (17°53'N, 78°27'E, 545.0 m), Parbhani (19°16'N, 67°47'E, 409.0 m), Latur (18°24'N, 76°36'E, 633.8 m), and Badnapur (19°50'N, 47°53'E, 519.6 m). Each entry was sown in a single row plot, measuring 4.2 m in length and spaced at 75 cm. The observations on pollen fertility (%) and other traits including days to maturity, plant height (cm), number of primary branches, seeds per pod, 100-seed weight (g) and yield per plant (g) were recorded on five randomly selected plants within each plot.

For studying pollen fertility five fully grown but unopened floral buds were harvested randomly from each plant between 1000-1400 hrs. The anthers from each bud were excised and squashed on glass slides and drenched with 2% aceto-carmin solution. Each slide was examined under light microscope in 3-4 microscopic fields and data on pollen fertility (Stained pollen grains) were recorded. A plant was considered male fertile if its $\geq 80\%$ pollen grains stained. The fertility data were transformed in to arc sin values and then analyzed using Genstat 12 edition. The stability parameters were estimated according to model proposed by Eberhart and Russell (1966).

RESULTS AND DISCUSSION

Genetic variability for pollen viability: The mean performance of genotypes (Parents and hybrids) for pollen fertility studied was analyzed statistically and the genotypic differences were found to be highly significant for individual location as well as pooled data. The location wise as well as pooled *per se* performance of parents, hybrids, and controls are given in (Table 1) and were compared by using respective critical difference at 5% and 1% level of significance. At Patancheru, 31 out of 37 parents showed 100% pollen fertility and were found superior as compared to the controls BSMR 736 (97%) and ICPH 2671

Table 1. Analysis of variance for individual location and over locations for pollen fertility

S.V.	Pollen fertility (%)				
	ICRISAT	Parbhani	Latur	Badnapur	Pooled
Genotype	638.95**	424.51**	200.45**	184.47**	443.43**
Replication	0.86	2.96	41.49	127.14**	1.19
Error	9.30	8.39	9.54	9.03	9.06

Table 2. Pollen fertility (%) of the hybrid combinations (3 lines x 34 tester) evaluated at four locations

Testers	Cytoplasmic-genic male-sterile lines														
	ICPA 2043					ICPA 2047					ICPA 2092				
	E1	E2	E3	E4	M	E1	E2	E3	E4	M	E1	E2	E3	E4	M
BSMR198	90	68	73	90	80	57	90	66	76	72	37	84	67	74	65
BSMR846	90	66	90	90	84	90	90	70	72	80	63	90	90	90	83
BSMR164	75	70	90	90	81	65	61	90	66	70	59	82	66	90	74
BDN 2001-6	65	90	90	90	84	71	69	90	90	80	57	66	65	59	62
ICP3525	90	90	90	90	90	39	76	90	71	69	77	56	72	60	66
BSMR175	90	90	90	90	90	36	38	90	68	58	73	71	58	90	73
BSMR2	90	90	90	90	90	69	90	70	47	69	58	90	71	70	72
ICPL12749	67	67	84	90	77	90	51	76	75	73	71	63	66	53	63
BSMR203	69	61	66	73	67	44	38	90	72	61	90	90	84	68	83
BWR154	90	38	90	90	77	36	71	63	90	65	84	62	78	90	79
BSMR571	63	90	64	68	71	63	63	90	90	77	80	90	78	70	80
ICP13991	39	42	60	90	58	80	66	74	68	72	50	67	78	84	70
ICP10934	90	90	90	90	90	90	70	74	67	75	67	62	90	90	77
HPL 24-63	73	90	90	90	86	90	61	74	90	79	56	90	75	73	73
AKT 9915	78	73	60	90	75	90	90	64	90	84	43	84	90	73	73
ICP 10650	90	90	90	90	90	65	66	84	90	76	44	65	90	74	68
ICP 3407	71	90	66	90	79	76	90	82	90	84	55	90	90	61	74
ICP3475	29	73	90	70	65	56	66	84	61	67	66	65	90	67	72
BSMR736	71	41	90	90	73	90	74	69	90	81	66	90	90	90	84
TV-1	90	90	90	90	90	90	64	71	90	79	90	70	90	90	85
AKT8811	90	90	75	76	83	90	90	72	90	85	78	72	90	68	77
PHULE T-00-1-25-1	53	90	80	90	78	72	71	76	66	71	74	62	90	77	76
PHULET-04-3-1	90	90	63	90	83	73	57	82	84	74	76	90	90	90	86
AKT 9913	65	46	90	90	73	56	71	66	61	63	90	68	75	90	81
AKT222521	68	53	90	58	67	70	84	54	69	69	90	84	61	62	74
AKT 00-12-6-4	58	90	70	75	73	60	70	82	90	75	40	68	90	74	68
ICP 3963	63	90	90	90	83	63	78	61	90	73	77	70	90	72	77
PHULE T-00-5-7-4-1	51	90	59	90	73	34	70	80	48	58	76	42	71	70	64
VIPULA	67	72	90	90	80	68	84	90	66	77	73	46	82	72	68
PHULE T-00-4-11-6-2	63	90	63	54	67	66	84	90	74	79	64	84	90	90	82
ICP11376	63	57	70	73	66	73	76	75	65	72	50	90	90	90	80
ICP3514	61	90	84	90	81	58	90	77	74	75	90	90	90	90	90
ICP3374	62	65	70	76	68	76	76	59	84	74	90	66	90	90	84
ICPL20106	90	90	65	82	82	81	78	83	82	81	90	72	90	90	85
Range	29-90	38-90	59-90	54-90	58-90	34-90	38-90	54-90	47-90	58-85	37-90	42-90	58-90	53-90	62-90
Average					81					82					89

E1 = Patancheru, E2 = Parbhani, E3 = Latur, E4 = Badnapur and M = Mean

(99%). Likewise, 22 parents at Parbhani and at Latur; and 14 at Badnapur exhibited 100% pollen fertility. The analysis of pooled data revealed that only four parents *viz.*, BSMR 846, BSMR 164, HPL 24-63, and PHULE T-00-1-25-1 showed 100% pollen fertility.

Fertility Restoration of the CMS Lines

ICPA 2043 crosses: None of the ICPA 2043n derived cross combinations maintained complete male sterility. There was a considerable variation for pollen viability across the four locations. The pollen fertility among the 34 hybrids involving ICPA 2043 ranged from 29 to 90% at Patancheru; 38 to 90% at Parbhani; 59 to 90% at Latur; and 54 to 90% at Badnapur (Table 2). Overall, the mean pollen fertility of ICPA 2043 crosses at the four locations was 81%. At Patancheru out of 34 testers used, 12 restored full pollen fertility of the hybrids. Similarly, 25 genotypes at Badnapur, 19 each at Parbhani and Latur restored the pollen fertility of the hybrids. The remaining hybrids at all the four locations

were partially fertile. On average, 15 (Cross check with table) genotypes (BSMR 846, BSMR 164, BDN 2001-6, ICP 3525, BSMR 175, BSMR 2, ICP 10934, HPL 24-63, ICP 10650, TV 1, AKT 8811, PHULE T-04-3-1, ICP 3963, ICP 3514 and ICPL 20106) recorded $\geq 80\%$ pollen fertility of ICPA 2043 (Table 2).

ICPA 2047 crosses: The fertility restoration of ICPA 2047 derived hybrids ranged between 34 to 90% at Patancheru; 38 to 90% at Parbhani; 54 to 90% at Latur; and 47 to 90% at Badnapur. The pollen fertility data recorded at Patancheru revealed that eight genotypes restored full pollen fertility of the hybrids. At Parbhani 10 hybrids and 15 hybrids at Latur and Badnapur were fully fertile. The remaining hybrids at the four locations were partial restorers. The mean values across the four locations revealed that seven genotypes (BSMR 846, BDN 2001-6, AKT 9915, ICP 3407, BSMR 736, AKT 8811 and ICPL 20106) were fully fertile, while the remaining ICPA 2047 hybrids with other testers were partial restorers (Table 2).

ICPA 2092 crosses: The pollen fertility among ICPA 2092 derived hybrids ranged from 37 to 90% at Patancheru; 42 to 90% at Parbhani; 58 to 90% at Latur; and 53 to 90% at Badnapur. Eight hybrids at Patancheru, 15 at Parbhani, 20 at Latur and 15 at Badnapur were fully fertile. The rest of the hybrids at these locations were partially fertile. Overall, 12 testers BSMR 846, BSMR 203, BSMR 571, BSMR 736, TV 1, PHULE T-04-1-3-1, AKT 9913, PHULE T-00-4-11-6-2, ICP 11376, ICP 3514, ICP 3374, and ICPL 20106) were classified as fertility restorers of ICPA 2092 while the remaining hybrids were partial restorer (Table 2).

Fertility restoration across CMS lines and locations: A perusal of entire pollen fertility data recorded in this study showed that none of the 34 testers maintained complete male sterility across with any CMS line at any location. This suggested that each and every tester used in crosses had some fertility restoring factor (s). At Patancheru, 12 testers with ICPA 2043, 8 each with ICPA 2047 and ICPA 2092 and at Latur, 25 testers with ICPA 2043, 14 with ICPA 2047 and 20 with ICPA 2092 were found to restore fertility. Nineteen testers with ICPA 2043, 13 with ICPA 2047 and 19 with ICPA 2092 restored the fertility at Parbhani. At Badnapur, 19 testers with ICPA 2043, 10 with ICPA 2047 and 15 with ICPA 2092 produced fertile hybrids.

Assessment of fertility restoration across CMS lines and locations together showed that with ICPA 2043, 17 testers restored full pollen fertility at all the four locations. Similarly with ICPA 2047, only seven restored the fertility at all the four locations and these were BSMR 846, BDN 2001-6, AKT 9915, ICPL 3407, BSMR 736, AKT 8811 and ICPL 20106. Interestingly, 12 testers with ICPA 2092 produced fully fertile hybrid at all the four locations. Over one dozen testers restored the fertility at three out of four locations. The data also showed that out of 34 testers evaluated, only AKT 8811 fully restored the pollen fertility of both ICPA

2043 as well as ICPA 2047. BSMR 736, on the other hand, fully restored the fertility of ICPA 2047 and ICPA 2092. Five tester genotypes (TV 1, BSMR 846, PHULE T-04-1-3-1, ICPL 20106 and ICP 3514) restored the pollen fertility in the hybrids derived with ICPA 2043 and ICPA 2092. In the present study the mean pollen fertility of crosses with the three CMS lines and 34 testers was more or less similar. However at individual performance level, majority of the combinations behaved differently in different environments with respect to pollen fertility and there was no trend was observed. This could be due to the different types of interactions between the nuclear genetic backgrounds of the male and/or female parents. Besides this, variable influence of local environment on the hybrid genotype also cannot be ruled out.

Significant variation was also observed in fertility restoration among the hybrids derived by crossing the same female and different male parents within and across the locations. This corroborates the observations reported earlier by Saxena and Kumar (2003), Saxena *et al.* (2005) and Nadarajan *et al.* (2008) in pigeonpea; Worstell *et al.* (1984) in sorghum (*Sorghum bicolor*) and Jan *et al.* (2002) in sunflower (*Helianthus annuus* L.). They attributed it to the presence or absence of one or more fertility restoring gene(s) in the testers.

The pollen fertility data recorded in this study were also subjected to stability analysis. The results showed that the fertility of individual tester varied considerably over different CMS lines and locations. On the basis of regression coefficient (bi) and mean square deviation (S^2_{di}) from regression of the hybrids it was revealed that out of 102 cross combinations evaluated, only 16 were found to be highly stable with unit regression and $S^2_{di} = 0$. These included crosses of ICPA 2043 with BSMR 2, 175, TV 1, Vipula, AKT 8811, HPL 24-63, ICP 10934, ICP 3525 and ICP 3407. Similarly, crosses of ICPA 2047 with BSMR 846, AKT 12-6-4, ICP 10650 and ICP 3374 and crosses of ICPA 2092 with ICP 3514 and PHULE 1-3-1 were also found to highly stable with respect to pollen fertility restoration of the stable hybrids identified, 13 had pollen fertility above the mean (76%) value and their restorers were considered good males for hybrid breeding with wide adaptation. On the contrary, only two hybrids had below mean pollen fertility and such combinations can be targeted for stressed environments (Eberhart and Russell 1966).

Evaluation of hybrids across environments revealed that none of the crosses completely maintained the male sterility. However, a number of crosses were partially male sterile and this type of expression is conditioned by some deleterious interactions between the cytoplasmic and nuclear genomes (Kaul 1988). He also concluded that the male fertility of the hybrids made on the CMS plants is restored when some specific fertility restoring nuclear genes, often one or two in number, are transmitted from

male (Restorer) parent. Such genes have ability to overcome the ill effects of sterility-producing genomic interactions.

At molecular level, the inter-genomic interactions controlling the expression of male sterility/fertility are highly complex and fragile in nature; and therefore, can be influenced by different environmental factors such as temperature, photo-period, radiation, plant nutrition etc. (Kaul 1988). In pigeonpea the mean temperatures during flowering period play an important role in floral bud initiation/development, and pollen production and their fertility (Turnbull *et al.* 1981). Sawargaonkar (2011) observed that during flowering period of the experiment the mean temperatures at all the four test locations ranged between 22-33°C and this could have played a possible interactive role in the development of fertile pollen grains.

Saxena *et al.* 2011 reported that in pigeonpea hybrids the expression of male fertility varied considerably at different locations characterized by a significant variation in the mean temperature. They also concluded that the hybrids with a single dominant fertility restoring gene were unstable with respect to pollen fertility across the locations. On the contrary, the hybrids carrying two dominant fertility restoring genes exhibited high levels of pollen fertility under in the same environmental conditions. Kaul 1988 also recorded similar observations and concluded that Instability in fertility restoration in the hybrids can occurs when restorer lines do not carry the entire set of dominant fertility restoration genes. In maize for example, four fertility restoring genes were reported and the presence of two genes in an individual resulted in partial restoration of male sterility (Wise *et al.* 1999). In an experiment Kennel *et al.* 1987 demonstrated that the absence of a single major fertility restoring gene in a hybrid plant reduced the male fertility causing proteins by 80%. The fertility restoration has also been associated with genes encoding pentatricopeptide repeat proteins (Hanson and Bantolila 2004). According to Kaul, 1988 once a male line is crossed with male sterile line, its dominant fertility restoring nuclear gene produces certain proteins which repair the damage of defective mitochondrial genome and make the hybrid plant male fertile. These interactions may be due to complementation, inhibition, epistasis, etc.

Saxena *et al.* 2011 reported that in pigeonpea the fertility restoration in A₄ CMS system was controlled by

two duplicate dominant genes; and the presence of either or both the genes restored pollen fertility. The hybrid plants carrying both the dominant fertility restoration genes demonstrated full and stable fertility restoration; On the contrary, plants with only one fertility restoring gene produced scanty and sticky pollen grains at some locations leading to partial male fertility. They concluded that such genotypes were more prone to genomic-environmental interactions. Dundas *et al.* 1981 showed that the partial male fertility/sterility in pigeonpea was a consequence of interruption in the process of microsporogenesis and these results in the partial collapse of tetrads.

Selection of hybrid parents: Considering the shrinking resources and requirements of high yielding cultivars, it is important that the breeding programmes should have sharp objectives and smart breeding approaches. To achieve these, it is imperative that the best possible parental materials be selected to launch the breeding activities. The selected parent genotypes should have traits like high productivity, high combining ability and resistance to major biotic and non-biotic stresses, besides the key market-preferred traits. In case of hybrid breeding, the highest priority of a pigeonpea breeder should be to introduce fertility restoring gene (s), which can sustain the vagaries of various external factors. Further, for wider adaptation of hybrids, it is also necessary that they have high level of resistance to most common fungal (*Fusarium udum*) and viral (Sterility mosaic) diseases. Therefore in the present study, traits such as pollen fertility restoration, disease resistance, key agronomy and market-preferred traits were given priority in selection; and AKT 8811, BSMR 736, TV 1, BSMR 846, PHULE T-04-1-3-1, ICP 3514 and ICPL 20106 were identified as potential male parents for breeding pigeonpea hybrids (Table 3). These lines were not only stable for fertility restoration across the three male sterile lines and four locations, but also expressed significant SCA effects in specific cross combinations. This group of testers also represented a considerable genetic variability by representing different heterotic groups (Table 4). The selected seven male and three female parents would provide good opportunities to breeders to develop medium duration high yielding pigeonpea hybrids for local and broad adaptation. The development of the high yielding CMS based commercial hybrids will provide an opportunity of

Table 3. Key traits of the male fertility restoring lines identified for hybrid breeding in pigeonpea

Genotype	Origin	Mat. (days)	Height (cm)	100 seed wt. (g)	#Wilt (%)	#St. mos (%)	Primary bran.	Seeds/pod	Yield g/plant
AKT 8811	Maharashtra	150	190	9.2	0.0	0.0	12	3.7	80.0
BSMR 736	Maharashtra	180	182	10.9	0.0	0.0	11	3.3	90.6
BSMR 846	Maharashtra	176	169	9.9	0.0	0.0	09	3.7	46.2
Phule 1-3-1	Maharashtra	168	222	10.6	0.0	0.0	10	3.5	48.7
TV 1	Maharashtra	170	190	11.5	0.0	0.0	11	3.7	153.6
ICP 3514	Uttar Pradesh	175	187	11.7	0.0	0.0	10	3.7	81.5
ICPL 20106	ICRISAT	182	283	11.9	4.0	1.0	19	4.1	91.3

data from disease sick nursery at Patancheru.

Table 4. Pollen fertility, specific combining ability effects and heterotic groups of the selected genotypes

Genotype	Het. group	Pollen fertility (%)		
		ICPA 2043	ICPA 2043	ICPA 2043
AKT 8811	I	83 (26.5**)	85 (NS)	77 (NS)
BSMR 736	I	73 (18.0**)	81 (11.1**)	84 (NS)
ICP 3514	I	81 (7.5**)	75 (NS)	90 (NS)
Phule 1-3-1	V	83 (5.1**)	74 (NS)	86 (8.4**)
TV 1	V	90 (6.4**)	79 (NS)	85 (7.8**)
BSMR 846	VI	84 (NS)	80 (16.0**)	83(14.6**)
ICPL 20106	VII	82 (17.2**)	81 (3.6**)	85 (7.9**)

(**) SCA effects; source: Sawargaonkar (2011)

achieving the long-cherished goal of breaking the yield barrier in pigeonpea.

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